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## Assortative mating in *Drosophila melanogaster* and among three species of the *melanogaster* subgroup

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*Document Version*

Publisher's PDF, also known as Version of record

*Publication date:*  
1988

[Link to publication in University of Groningen/UMCG research database](#)

*Citation for published version (APA):*

van den Berg, M. J. (1988). Assortative mating in *Drosophila melanogaster* and among three species of the *melanogaster* subgroup. s.n.

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## Summary

An animal will often not mate at random with potential mates. Besides the obvious choice for conspecifics, animals also often choose their mates within a species. This intra-specific mate choice exists in many varieties, such as choosing a certain phenotype, a non-related mate, or a rare mate. This study concerns one of these i.e. assortative mating, in which certain phenotypes mate either more often with each other than expected under random mating (positive assortative mating, P.A.M.), or less often than expected (negative assortative mating, N.A.M.). N.A.M. may result in inbreeding avoidance, while P.A.M. may contribute to reproductive isolation between groups of a species, and therefore even contribute to the onset of speciation. This thesis aims at addressing the following questions: can assortative mating be demonstrated in *Drosophila melanogaster* and, if so, what are the underlying mechanisms?; what are the underlying mechanisms of P.A.M. among three closely related species of the *melanogaster* subgroup i.e. *D. melanogaster*, *D. mauritiana* and *D. simulans*? and lastly, what is the role of P.A.M. in speciation?

*D. melanogaster* has been chosen as the primary study object as this organism has been thoroughly studied and the sexual signals and behavior are also well known. Furthermore, this species is very easy to breed and the existence of the very closely related species makes it possible to analyse P.A.M. in detail not only at the intra-specific level but also inter-specifically. This facilitates a study of the role of P.A.M. in speciation.

In Chapter 1 a survey of the sexual behavior and signals is given. When a male *D. melanogaster* encounters a conspecific female, it often touches this female with his tarsi. By doing this it probably perceives the female sex pheromone. This pheromone consists of a mixture of linear alkenes and alkadienes (in *D. melanogaster*), but in *D. mauritiana* and *D. simulans* pheromones, only alkenes are present. When the pheromone is perceived, a male often starts to vibrate his wings, which is accompanied with a species-specific song. This song may stimulate the females to accept the males' copulatory attempts. Furthermore, the male can also lick the females' genitalia, which probably acts as a tactile stimulus. Thus several signals and behavior elements are present to form a basis for both sexes to choose their mates in such a way as to result in assortative mating. In fact both N.A.M. and P.A.M. were found in *D. melanogaster*.

At first sight the N.A.M. found in Chapter 2 seemed to confirm the hypothesis of Averhoff and Richardson {(1974) Behav. Genet. 4: 207-225}. These authors explained the N.A.M. found in their mass mating experiments between inbred lines as follows: males were thought to be unresponsive to their own volatile substances, due to continual saturation

of chemoreceptors. In inbred lines, males will also be unresponsive to such substances from their own genetically similar sibs, but they will be responsive to those from non-related females. The mass mating experiments described in Chapter 2 also showed N.A.M. in one combination of lines. However, detailed behavior observations, never gave any evidence of the kind of mechanism underlying mate choice as predicted by the hypothesis of Averhoff and Richardson (1974). Instead there was evidence that N.A.M. was most likely caused by an interaction of interstrain differences in male vigor and female reluctance.

To test this last hypothesis a model for the sexual behavior of *D. melanogaster* was constructed (Chapter 3). Males were assumed to court females with a certain intensity (male vigor, V). This courtship would be summated by a female until a particular threshold was reached (female reluctance, R). Both variables were considered to be gamma distributed. The resulting copulation latency times (C.L.T.) of single pairs will then be given by the formula  $C.L.T. = R/V$ . This model describes the C.L.T.'s of single pairs very well, which confirms the validity of the model. Moreover the data of the mass mating experiments of Chapter 2 proved to fit this model completely, thus the N.A.M. found could be fully explained in terms of interstrain differences in male vigor and female reluctance.

In Chapter 4 a case of P.A.M. is described between two strains, one of which (Malawi) had a very deviant sex pheromone, whereas the females of the other strain (Bogota) had a "normal" pheromone. Using gas chromatography and mass spectrometry it was shown that the configuration and/or the position of the double bonds of the predominant Malawi pheromone component deviated from "normal". Although such deviations of sex pheromones usually have drastic effects on sexual behavior in many other insects (e.g. Lepidoptera), the polymorphism found here did not result in male mate choice.

The P.A.M. found in Chapter 4 is more likely based on female mate choice than on male mate choice. Therefore the courtship sounds of both Malawi and Bogota males were studied and these were found to be different (Chapter 5). However, this was also not the cause of the P.A.M. found in Chapter 4. Lastly, differences in the sexual behavior of both sexes were found. Both Malawi males and females moved much less during courtship than their Bogota counterparts. This resulted in a nearly complete lack of copulations in mass mating experiments between the readily moving Bogota females and Malawi males which did not follow. Thus the number of inter-strain matings was lower than expected under random mating.

In Chapter 6 the underlying mechanisms of the inter-specific P.A.M. found between *D. melanogaster*, *D. mauritiana* and *D. simulans* are examined. Differences in sex pheromones were found to play a major role in two out of the three combinations (*D. melanogaster* versus *D. mauritiana* or *D. simulans*). However, these differences did not play any role in

the combination involving the two most closely related species (*D. mauritiana* and *D. simulans*). Differences in courtship sound seemed to play only a minor role in P.A.M. in all combinations. Moreover, also other, unidentified, mechanisms appeared to contribute to P.A.M. between these three species.

Based on the conclusions drawn in the previous Chapters a hypothesis is given (Chapter 7), concerning the way in which speciation starts in the *melanogaster* subgroup. If a few individuals become separated from their original population and a new population is founded, both hybrid depression and deviation of sexual behavior and/or signals may evolve quickly, due to the founder effect. Later, the females of the derived population will be selected in such a way that they refuse the copulatory attempts of males from the original population. These effects, if operating together, may provide the onset of speciation.

## Samenvatting

Een dier zal zelden willekeurig paren met potentiële partners. Afgezien van de voor de hand liggende keuze van soortgenoten, heeft een dier vaak ook binnen de soort bepaalde voorkeuren. Deze keuze tussen soortgenoten kan verschillende vormen aannemen, zoals een voorkeur voor een bepaald fenotype, een niet nauw verwante partner, of een type partner dat zeldzaam is. Deze studie handelt over een van deze typen, n.l. assortatieve paring, oftewel: een vorm van partnerkeuze waarbij bepaalde fenotypen meer met elkaar paren dan op grond van toeval verwacht wordt, (positieve assortatieve paring, P.A.P.) of juist minder dan verwacht (negatieve assortatieve paring, N.A.P.). N.A.P. is een vorm van partnerkeuze, die kan leiden tot het vermijden van inteelt, terwijl P.A.P. kan bijdragen tot een reproductieve isolatie tussen groepen binnen een soort, en daarom kan bijdragen tot soortsvorming. Dit proefschrift is gebaseerd op de volgende vraagstellingen: kan assortatieve paring aangetoond worden in *Drosophila melanogaster* en zo ja, wat zijn dan de achterliggende mechanismen? wat zijn de mechanismen achter P.A.P. tussen drie nauw verwante soorten van de *melanogaster* subgroep (dit zijn *D. melanogaster*, *D. mauritiana* en *D. simulans*)? en wat is de rol van P.A.P. bij soortsvorming?

*D. melanogaster* is gekozen als belangrijkste studie object, omdat dit organisme al uitgebreid bestudeerd is en de seksuele signalen en het seksuele gedrag inmiddels goed bekend zijn. Daarbij is deze soort eenvoudig te kweken en de aanwezigheid van de zeer nauw